knowledge. For this he is willing to do his utmost in any and every direction that is open to him. The motive which controls the philosophical skeptic is his fear of a false step. He is indisposed to stir at all until secure of his footing. The mind when in a scientific attitude is patient even of known error, if only it can be made the basis of a really good working hypothesis that will help the inquirer forward, and which may then become susceptible of revision and correction. Numberless instances can be given in which this process has led to valuable results. In fact, most of man's scientific knowledge of nature is owing to it. But such a method is repugnant to the philosophical skeptic, whose attitude damps all advance unless it can be carried on from the beginning under conditions of perfection—in other words, under conditions which are impossible in the early stages of almost every inquiry.

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HINTS ON THE CLASSIFICATION OF THE ARTHROPODA; THE GROUP A POLYPHYLETIC ONE.

BY ALPHEUS S. PACKARD.

(*Read April 3, 1903.*)

Of the ten or twelve chief groups or phyla into which the animal kingdom is subdivided by systematists, nearly all except those of the old groups Vermes and the Arthropoda are acknowledged to be fairly well limited. There is a general agreement of opinion as to the naturalness and monophyletic origin of the Protozoa, Porifera, Cœlenterata, Echinodermata, Mollusca and Chordata. Those of the "worms" and the great group Arthropoda are still the cause of more or less difference of opinion.

The group Arthropoda was established by Siebold in 1848, but in late years, with the increase in our knowledge of the morphology and embryology of the Arthropodan classes, especially of the Trilobita, Merostomata, Malacopoda (Peripatus) and Myriopoda, there has been expressed by several zoologists the opinion that the Arthropodan phylum is a more or less artificial one, and should be subdivided into more natural groups—*i. e.*, that it is composed of several phyla.

Were it only a matter of convenience, the great group Arthropoda might be retained. The fundamental characters are the possession of jointed or polymerous appendages, and the great reduction or entire absence of a cœlomic cavity. Besides this the anterior body-segments are grouped into a head, while the trunk-segments may be either separate and homonomous or differentiated into a thoracic and abdominal region. But it has been pointed out by Kingsley and also by Laurie that the possession of jointed legs in the different classes may be due to convergence, or to homoplasy.

Kingsley and others have shown that the gills and tracheæ are adaptive characters, and that the retention of the groups Branchiata and Tracheata is not warranted. Gills and tracheæ are adaptive features. We have in the phylum Palæopoda the classes of branchiate Trilobita and branchiate Merostomes, while from the latter appear to have evolved the terrestrial tracheate Arachnida. The mode of respiration affords fair class characters, but not phylum characters.

HISTORY OF OPINION AS TO THE POLYPHYLETIC NATURE OF ARTHROPODA.

As early as 1869 the present writer[1] rejected Müller's (1864) and Haeckel's view (1866) that the insects and other tracheates had descended from the zoëa of the Crustacea, and claimed their ancestry from the Annulata. Kennel[2] in 1891 stated his view that the Crustacea arose by an independent line of descent from that of the Annelida, the two groups having diverged from a Preannelidan ancestor, his Protrochosphæra, from which the Mollusca also sprang. The tracheate classes he traces back to the Peripatiformes, from

[1] My views were stated in an article, entitled "The Ancestry of Insects," in the *American Naturalist*, iii, p. 45, March, 1869. In commenting on Haeckel's view that the ancestor of insects, spiders, and myriopods was a zoëa-like form, a view previously expressed by Fritz Müller, and also held by Dohrn, I rejected this theory and suggested that the ancestor of insects and other tracheates "must have been worm-like and aquatic." A little later I referred the ancestry of both the insects and crustacea, "independently of each other, to the worms (Annulata)" (*American Naturalist*, iv, p. 756, February, 1871).

[2] "Die Verwandtschaftverhältnisse der Arthropoden (*Schriften Naturf. Gesells. Dorpat*, vi, 1891). Kennel's view that the Nauplius form originated from the Rotatoria was earlier expressed by the writer, as follows: "The Nauplius form of the embryo or larva of all Crustacea also points back to the worms as their ancestors, the divergence having perhaps originated in the Rotatoria" (*American Naturalist*, v, p. 52, March, 1871).

which Peripatus arose, with two lines of descent, one ending in the Chilopoda and Insecta, the other in Diplopoda, Pauropoda and Symphyla, the branch finally ending in the Arachnoidea. He thus divides the Arthropoda into Branchiata (Crustacea) and Tracheata. He quotes Plate,[1] who in 1889 considered that Crustacea and the Tracheates followed each an "entirely separate developmental path," since he derived the Crustacea from the Rotatoria, and the Tracheata from the Annelida.

In 1883 Kingsley[2] inquired whether the group Arthropoda is a natural one, calling attention to the fact that the insects have been derived from Peripatus, while the Crustacea "had an ancestor resembling the Nauplius of the Phyllopoda or the Copepoda." In 1894[3] he divided the Arthropoda into three subphyla: I. Branchiata; II. Insecta or Antennata, and III. Diplopoda, rejecting the old grouping into Branchiates and Tracheates (though retaining the Branchiata), and he states his belief that the three divisions he makes "are but remotely related to one another, and it may yet be proved that they have no common ancestor nearer than the Annelids."

Indeed, as early as 1886, A. C. Oudemans[4] thus expressed his views as to the relations of Limulus with the trilobites, and of the derivation of the scorpion from the Eurypterida: "Though some zoologists doubt the relationship of Limulus with the Trilobita, the paleontologists have long ago been convinced of it. Among the numberless Trilobita there occur all possible transition forms between them and Limulus, and to Scorpio the Eurypterida form a partial bridge." His genealogical tree represents the Xiphosura as originating from the trilobites and the scorpions as derived from the Eurypterida, in this respect theoretically anticipating the results attained by Pocock with Palæophonus. Oudemans also acknowledges the close resemblance of trilobite larvæ to that of Limulus.

[1] "Ueber die Rotatorien fauna des bottnischen Meerbusens, nebst Beiträgen zur Kenntniss der Anatomie der Philodiniden und der systematischen Stellung der Räderthiere" (*Zeitschrift f. Wissen. Zoologie*, xlix, December, 1889).

[2] *American Naturalist*, xvii, p. 1034, 1883.

[3] *American Naturalist*, xxviii, pp. 118 and 220, 1894.

[4] "Die gegenseitige Verwandschaft, Abstammung und Classification der sogennanten Arthropoden" (*Tijdschr. d. Nederland. Dierk. Vereen*, 2e Ser. Deel 1, 1886).

I also stated in 1893[1] that there are four lines of development in the Arthropoda (throwing out for the present the Linguatulina and Tardigrada), viz.: "the Podostomatous line, the first to be struck off from the Annelidan stock (the trilobites being the first forms to appear); second, the Arachnidan line; third, the Crustacean line, nearly coeval with the first or Podostomatous; and the fourth, the line culminating in Myriopods, Scolopendrella and insects; and it is safe to suppose that the terrestrial tracheate groups of Arachnida, Myriopoda and insects were later products than the marine, aquatic branchiate classes—*i.e.*, the Podostomata and the Crustacea."

Afterwards in 1898, in my *Text-Book of Entomology*, as a result of the memoirs of Lankester, Kingsley, and the work of Kishinyoue on the embryology of the Japanese Limulus, from morphological and embryological data, having abandoned earlier opinions as to the Crustacean affinities of Limulus, I gradually was led to recognize the close affinity of the Merostomes and Arachnida, stating that the embryology of Limulus and Arachnida "shows that they have descended from forms related to Limulus, possibly having had an origin in common with that animal, or having, as some authors claim, directly diverged from some primitive eurypteroid merostome" (p. 6). Again, on p. 8: "The Arachnida probably descended from marine merostomes, and not from an independent annelid ancestry." Again, on p. 3, in a discussion of the relation of insects to other Arthropoda: "It is becoming evident, however, that there was no common ancestor of the Arthropoda as a whole, and that the group is a polyphyletic one. Hence, though a convenient group, it is a somewhat artificial one, and may eventually be dismembered into at least three or four phyla or branches."

Subdivision of the Arthropoda into five Phyla.—I would suggest the following grouping of the principal classes of the Arthropoda, beginning with what may be regarded as the most primitive assemblage of classes, and for which I would propose the name *Palæopoda*, in allusion to the very primitive and homonomous nature of their post-antennal or post-oral appendages, when compared with those of

[1] "Further Studies on the Brain of Limulus Polyphemus, with Notes on its Embryology" (*Memoirs Nat. Acad. Sciences*, p. 322, 1893). Compare also *Zoologischer Anzeiger*, April 20, 1891.

the Crustacea.[1] I also add what appear to be the essential characters of the phylum.

Phylum I. PALÆOPODA. Composed of three classes—*i. e.*, *Trilobita*, *Merostomata*, *Arachnida.*

Body trilobate (in Trilobita and many Merostomata), never protected by a true carapace, composed of a head and trunk region; the head-region separate from the trunk, in Trilobites (Triarthrus) composed of (judging by the appendages) five segments (somites, arthromeres), in Merostomes six, while in Arachnida the head fused with the so-called thorax (cephalo-thorax) also consists of six segments. The first pair of head-appendages, in a single trilobitic genus (Triarthrus), are long, slender, uniaxial and antenniform, or biramose, chelate (Merostomata and Arachnida); all the post-oral appendages, in the most primitive class (Trilobita), biramose, consisting of an outer and inner many-jointed division, but all homonomous, or retaining the same fundamental and primitive shape from the mouth to the end of the body, and never (as they are in Crustacea) differentiated into true or functional mandibles, maxillæ, maxillipedes, ambulatory uniaxial thoracic legs, or biramose abdominal limbs. The gnathobases, or coxal joint of each limb, especially those near the mouth, armed with inward projecting spines, acting as jaws to tear and to keep the food or prey from escaping. In the Merostomata the post-cephalic or trunk (abdominal) limbs biramose and adapted for swimming, and either (in Trilobites) expanded posteriorly and probably serving both for swimming and respiration, or in Merostomes (*Limulus*) bearing on the exopodite of each limb, except those of the first pair, a pile of numerous gill-sacs. In Arachnida, in adaptation to a terrestrial life, the six pairs of abdominal or trunk limbs are reduced, mostly atrophied, represented in the scorpion by the pectines and the four pairs of invaginated book-lungs, and in spiders by the two pairs of book-lungs (Mygale) and the three pairs of spinnerets, which are 2–3 jointed, external free appendages. A hypostoma is present and well developed in Trilobita and Merostomata, as also a double underlip, the chilaria of Limulus.

The eyes of Asaphus, etc., and of Limulus are compound, al-

[1] Palæocarida was proposed when I believed that Limulus and its allies were Crustacea; my name Podostomata was proposed for a group embracing the two classes Trilobita and Merostomes; the present name, Palæopoda, is needed to embrace the three classes mentioned.

ways sessile, and distinguished by the thick, either lenticular or long conical lenses, arranged in quincunx order.

The integument is chitinous, insoluble as in insects, never containing carbonate or phosphate of lime, or forming a solid crust as in the higher Crustacea. The cartilaginous plate (endosternite), so large and well developed in Limulus, is also present in Arachnida.

In the living forms (Limulus and Arachnida) the digestive canal may be differentiated into a slender œsophagus, a proventriculus armed with rows of numerous chitinous teeth (Limulus) and an intestine, the stomach being but slightly differentiated. The liver or hepato-pancreas is large and voluminous. In the Merostomes (Limulus) there are no salivary glands, though occurring in Arachnida. Genital openings always (Merostomata and Arachnida) prosogoneate, the oviducts or seminal ducts opening out separately on the posterior aspect of the basal abdominal limbs (Limulus), or in Arachnida united into a single terminal passage, opening by a single orifice at the base of the abdomen. In the marine forms, with gills or localized respiration, the heart is tubular and the arterial system remarkably developed and finely divided, whereas in the tracheate, terrestrial forms the arteries and veins are absent, respiration being carried on throughout the body (chiefly abdominal) cavity.

In the Palæopoda there is no true metamorphosis like that of the Crustacea, no nauplius or zoëa stage. The first or earliest larval stage, the *protaspis*[1] stage of Beecher, can, so far as we can see, in no way be likened to the nauplius of a crustacean. The nauplius has an oval body, not differentiated into segments, but with three pairs of slender swimming limbs, which finally become the two pairs of antennæ and the mandibles of the adult. In the protaspis of trilobites, as defined by Beecher, the conditions are entirely different and such as suggest the origin from a polymerous Annelid ancestor. The minute disk-like or suborbicular larva of different genera of Trilobites described by Barrande and by Beecher consist of two regions, a head and trunk or abdomen. There are in the head indications of five annulations, the same number as in the adult Triarthrus; the much shorter abdominal region has from "one

[1] This term was proposed by Beecher in his paper on "The Larval Stages of Trilobites" (*Amer. Geologist*, September, 1895). Previously to that, A. C. Oudemans, in 1886, in the article cited, proposed the name *Proagnostus* for the same stage. If used, this name might be amended to read Protagnostus stage.

to several annulations," which probably represent segments. From this we logically infer that in the protaspis of trilobites there were more than three pairs of head-appendages, and possibly two or three pairs of abdominal appendages. Now the larva of Limulus is hatched with two body-regions, of the same general shape as those of the trilobites, and it is also trilobed; the embryo, sometimes before hatching, with its thick spherical body, strongly recalls the protaspis stage of trilobites, and seems to justify the view that the freshly hatched larva of Limulus is a protaspis.[1] In the protaspis-like fossil Cyclus, which seems to represent an ancestral type of Limuloids persisting into the Carboniferous Period, there are traces of head-appendages like those of the embryo Limulus.

The metamorphosis of the Palæopoda is, then, incomplete; the limbs of the protaspis retain the form and functions of the larva, the adult simply differing in acquiring at successive molts additional trunk-segments, with their corresponding limbs.

The eggs of Limulus as well as of Arachnida are large and not so numerous as in some Crustacea; those of Limulus are laid in the sand. The eggs of trilobites are also large, spherical, and evidently, like those of Limulus, were deposited in the sand or sandy mud, as they occur separately from the trilobites themselves.

The embryology of Limulus presents some unique features, and yet there is such a close resemblance to that of the scorpion that the embryology of the Arachnida, as I have freely acknowledged, affords very strong proofs of their relationship to and descent from merostomes. In the embryo of the scorpion and spiders there are six pairs of head- (cephalothoracic) appendages, and the mode of origin of the book-lungs of the scorpion and spiders seems to prove that they are derivatives of the exopodites of the abdominal limbs of Limulus.

It results from what is now known of the structure of the Trilo-

[1] I freely acknowledge that many years ago (1872) I supposed that the embryo Limulus passed through a nauplius, and that I called it a "subzoëa stage," but this view was long since abandoned, as also my contention that Limulus was nearer the Crustacea than the Arachnida. It need hardly be added that while as previously I cannot agree with the view that Limulus is an actual Arachnid, it has for some years, through the result of the work of Kingsley and Kishinyoue, been evident that the Merostomes are closely related to the Arachnida, and I adopted this view in my memoir on the brain of Limulus (1893).

bita that they have no relationship with the Crustacea. To include them in that group, otherwise a most natural one, is not good taxonomy. The chief characters which are given for retaining the Trilobita as a primitive group of Crustacea are the presence of the antennæ-like preoral appendages of Triarthrus and one or two other genera. That this is not so important as might seem at first sight is the presence of four antennæ-like appendages in the head of Eurypterus; Holm having discovered that the first pair are chelate, like those of Limulus.

Both Trilobita and Crustacea have biramose limbs, adapted for swimming, but so has any marine arthropod; the fact that the limbs are divided is the result of their inheritance in either class from Annelids with parapodia, but in the multiarticulate structure of each ramus and the entire lack of differentiation of the whole series of postoral limbs in Triarthrus we have fundamental characters which are diagnostic of the Trilobites, and widely separate the class from the Crustacea. Whether the Merostomata are widely distinct from the Trilobita or not, we submit that it is a mistake to include the latter in the class of Crustacea.

Entirely disagreeing with those who widely separate the Merostomata from the Trilobites, after repeatedly going over the subject, the close relationship of the two groups seems to us to be very apparent, the differences being only such as would separate the two classes of a single phylum. It has seemed to us that the merostomes and trilobites either had a common ancestry, which was a protaspid, or the Merostomes by way of the Synxiphosura diverged from the trilobite stem after it had been established in Precambrian times. Thus far, unfortunately, we know nothing of the nepionic stage of any of the Eurypterida. Their earliest adult form (Strabops of Beecher[1]) occurs in the Cambrian, while the Synxiphosura date from the Silurian. It is not improbable that some genus of this group gave origin to the Xiphosura. On the other hand, is there not so close a resemblance between some of these Synxiphosura, such as Neolimulus and Bunodes, as to suggest that the Merostomes are direct descendants of the Trilobita? If we compare the figures

[1] Although Beecher refers this early form to the Eurypterida, it appears, judging from his figure, to quite as much resemble certain Synxiphosura, as Bunodes and Neolimulus, in the short, broad head and shape of the trunk-segment and telson, though it has two segments more than in the Synxiphosura and one segment less than in the Eurypterida.

of *Aglaspis eatoni* with that of Dalmanites (Figs. 1414 and 1331 of Zittell-Eastman's *Paleontology*), is there not such a close resemblance in the shape of the head (or cephalothorax) and of the trunk-segments as to suggest a close alliance, even though members of two distinct classes? To answer this question by saying that this is a case of convergence, the objector might be referred to the other Synxiphosura, which also suggest a common origin of the two classes from a protaspis ancestor. It has been suggested that some of the Cyclidæ are larval Eurypterida or Limuloids; if this should prove to be the case (of which we are by no means sure, as no Cyclidæ have yet been found below the Carboniferous), we should have an additional argument for the common origin of the two classes, for the Cyclidæ somewhat resemble the larval trilobites.

Relation between the Merostomata and Arachnida.—While we have from the first maintained that the Merostomes should not actually be included among the Arachnida—*i. e.*, that Limulus is not a genuine Arachnidan, as claimed by Van Beneden, Lankester and later authors—from the evidence we now have as to the mode of origin of the book-lungs and the morphogeny of the appendages in general, and especially the interesting and remarkable discovery by Mr. Pocock,[1] that the Silurian so-called scorpions are probably marine links between scorpions and Eurypterida, whatever objections I have formerly expressed to their Arachnidan affinities are now overcome, and it seems plain that the scorpion is a direct descendant of some Eurypteridan. Pocock's fortunate discovery in the Silurian scorpion (*Palæophonus hunteri*) of the inner branch of a two-jointed appendage, which appears to be the homologue of a recent scorpion's "pecten," should it be confirmed by the discovery of additional examples; as well as the thickness of the head-appendages, the last four pairs of which end in a single point, not in claws, as in modern scorpions—these discoveries appear to give the clue to the line of descent of Arachnida from some Merostome, one would say from some Eurypterus-like form, though, from other features observed by him, Mr. Pocock takes the view that "Palæophonus occupies an intermediate position between Limulus and the Eurypterida on the one hand and recent scorpions on the other, standing, if anything, rather nearer to the former than to the latter."

[1] "The Scottish Silurian Scorpion," *Quart. Journ. Micr. Sc.*, Vol. 44, n. s., 1902.

We quite agree with Pocock's opinion that Palæophonus was not adapted for land and aërial respiration, but "lived in the sea, probably in shallow water, its strong, sharply-pointed legs being fitted for maintaining a secure hold on the bottom."

In conclusion, then, we would suggest, from our present knowledge of the Palæopoda, that the group is a natural one, that the line of descent of the phylum from some Annelid-like worm was independent of that of the crustacean phylum, and that the affinities shown by morphology and embryology to exist between the Trilobita, Merostomata and Arachnida are so close that they form a tolerably definite series of interrelated classes.

Phylum II. PANCARIDA. Represented by a single class, *Crustacea.* The phylum name is proposed for the reason that the group is so well circumscribed, none but the genuine Crustacea or Carides belonging to it, forms as to whose position in nature all zoologists are well agreed.

In this group there is a decided advance over the Palæopoda in the differentiation of the appendages into from three to six kinds, with corresponding functions. In the lower or more primitive, though somewhat modified, group of Cladocera, such as Daphnia, there are two pairs of antennæ, a pair of mandibles, of maxillæ, and of legs or trunk-appendages, the whole performing four different functions; while in the Decapoda there are besides the antennæ, mandibles and maxillæ, three pairs of maxillipedes, five pairs of thoracic and six of abdominal legs, or appendages, in all performing six different kinds of functions—a degree of differentiation and specialization not exceeded by any other Arthropodan group.

The members of the phylum show an increasing tendency, as we rise towards the more specialized forms, to a heteronomous segmentation and also to a wonderful transfer of parts headwards (cephalization), the cephalothorax being covered by a carapace formed by the hypertrophy or excessive development of the tergites of the second antennal and mandibular segments. In the Phyllocarida the cephalothorax is covered by a bivalvular carapace, with a weak adductor muscle; while in Apus it, in adaptation to its burrowing in soft mud, assumes the general shape of the shield of Limulus; while in the Estheridæ the entire body is protected by the two valves, which are connected by a definite hinge and ligament. On the other hand, the head-shield of the Palæopoda, as well as the pygidium when occurring, is the result of the simple fusion of the segments. While the Phyllopoda are generally regarded as the most primitive group—their swimming limbs closely resembling those of Annelid worms—it may be questioned whether the Phyllocarida are not a still more primitive group; certainly they are the most composite or synthetic, and were the earliest known group of Crustacea.

Crustacea are, like the Palæopoda, prosogoneate; but when we take into account the fact that there is in the adult but a single pair of nephridia (the green gland), or in other forms (Phyllopoda) the shell gland, there has been a great reduction in the number of pairs from what may have been the ancestral type, while Limulus still retains four pairs. In all Crustacea the eggs are carried attached to the body of the parent, and never, as in trilobites and merostomes, deposited loosely in the sand.

In their metamorphosis, which is a complete one in all the typical forms, the larval stage of the lower Crustacea being a nauplius, we have another feature wanting in the Palæopoda. As is well known, the early embryo of Moina passes through a prenauplian stage like that of Annelida, and the indications are that the nauplius is itself a derivation from the trochosphæra stage of Annelid worms.

Now, as is well known, the most primitive groups or members of a group do not undergo transformations; and in this respect the Pancarida are a later, more specialized group than the Palæopoda. It will be remembered that the most primitive insects (Synaptera) do not undergo a metamorphosis, and in several of the lower orders of winged insects it is incomplete, there being no larval and pupal stages; in the Arachnida only the extremely modified Acarina undergo a slight metamorphosis. That of the Meropoda is slight.

Enough has been stated, we think, to show that the Palæopoda are quite remote from the Pancarida, and that a union of the trilobites in the same class with the Crustacea brings about an unnatural association, and tends to an unnecessary amount of confusion.

Dr. Kingsley regards the Trilobita as the more primitive subclass of Crustacea, but we are unable to see any features in Crustacea which could have been derived from trilobites; there are no transitional forms, and the larval forms are widely distinct, as he has well shown. The gap between the two groups is, on morphological and embryological grounds, a very wide one. Already in the early Cambrian seas trilobites were a predominant type, while the Crustacea were comparatively scanty in numbers, and represented by primitive types showing no trace of trilobite characters.

The Chief Factors in the Evolution of Classes.—Assuming that the Arachnida, represented by the most typical form, the scorpion, have evolved from the class of merostomes, in the way suggested by Pocock, the entire process or phenomenon has the most direct and instructive bearings on the method of evolution of one class from another.

In the first place, the single group of scorpions—say a single generic form—appears to have arisen from some genus of Eurypterida, allied to Eurypterus, and by divergent evolution the great class of Arachnida, with its eight orders, appears to have originated by one step after another from a single type, not necessarily an individual, but many, all the members of the genus being modified by similar causes, in the same manner and at the same time.

The modification of a marine Eurypteroid form, perhaps living in a shallow, land-locked basin, perhaps finally becoming brackish, into a terrestrial scorpion, was due to changes in the environment, in the topography; this reacted on the Eurypterid and resulted in change of habits, and consequent adaptation to brackish, and perhaps to fresh, water, and finally to land. With little doubt, all the forms inhabiting the area underwent the same kind of modification and similar adaptation to a new medium, the same changes of function resulting in the disuse of organs adapted for marine existence and the evolution of structures adapting the animal for terrestrial life.

The changes by which the connecting links (Palæophonus) became transformed into a genuine scorpion, the ancestor and founder of the Arachnida, were the following:

1. The loss by disuse of the abdominal swimming appendages (except the pectines), and the ingrowth and reduction by disuse of the expodites, the gills attached to them being carried in, forming eventually the book-lungs of the scorpion, each with its spiracular opening, adapted for aërial respiration.

2. The four hinder pairs of cephalothoracic appendages became slenderer after the animal had left the water and adopted a life on land, under stones or the bark of trees, etc., and the single stout claw of the original Palæophonus became by use, in climbing trees, etc., two-clawed, like those of all Arachnida and insects.

3. The compound eyes of the Merostomes became broken up into groups of single eyes.

4. Most remarkable changes took place in the internal organs, resulting in the development of salivary glands, none occurring in Crustacea and other marine Arthropods.

5. The acquisition of Malphigian or urinary tubes which exist in terrestrial Arthropods, Arachnida, insects, etc., but in no marine Arthropods.

6. A gradual reduction in the number of pairs of nephridia, all Arachnida having but a single pair, Limulus having four pairs, and the Eurypterida presumably as many.

7. After the scorpion type became fixed and the spiders arose, the number of pairs of book-lungs became reduced from two pairs in Mygale to one in other spiders, and then began an evolution of tracheæ from dermal glands—a process seen in certain terrestrial planarian worms as well as land-leeches.

8. While the arterial system of Limulus, owing to its localized organs of respiration, is remarkably developed, in the scorpion the arterial system is greatly reduced, and in the tracheate Arachnida, such as the spiders, there are no arteries or venous lacunæ.

It is most probable that the evolution of the Palæophonus descendants, viz., the scorpions of the Carboniferous—assuming that they were true scorpions—took place with comparative rapidity, *i. e.*, by tachygenesis, without the extremely slow method postulated by the natural selectionists, the modification suggested above having contemporaneously affected all the individuals, many thousands or tens of thousands alike. The method was not, as Darwin imagined, the result of a single chance variation gradually and by numberless intermediate forms passing into a species which gave origin to many others, from which were gradually evolved new subgenera, genera, subfamilies and so on, but the method was radically different. The Palæophonus, an Eurypterid, became, we take it, in a comparatively few generations the parent of a scorpion, the representative of a distinct class. The class characters, great as are the differences, especially in its internal organs, between an Arachnid and a Merostome, were assumed with comparative suddenness. New classes, like new species, did not arise from a single but from a large number of individuals. This was Lamarck's doctrine, and it has been reaffirmed by De Vries. This shows that even classes are in a degree artificial or ideal conceptions. And so it was with the evolution of mammals from theromorphous reptiles, and of birds such as the Archæopteryx from reptiles. With our present knowledge we can trace an almost exact parallel between the tachygenic origin, by change in the medium, inducing changes in habits and the functions, of flying in sectsfrom Synapterous forms, that of the Arachnida from the Merostomes, of Amphibia from Ganoid fishes, of reptiles possibly from Amphibia like the Labyrinthodonts, of birds from dinosaurian reptiles, and of mammals from theromorph reptiles (unless the Amphibians, as some contend, were the source of mammalian life).

The exciting causes of the differentiation of classes, as well as orders, families and genera, were geological and topographic changes, enforced migration and consequent isolation, adaptation to a new medium, to new conditions of life, such as a change from marine to fresh water, from fresh water to land, and in the case of pterodactyls, birds and insects, from a terrestrial life to one spent partly in the air.

The early Paleozoic ages as well as the Precambrian were periods of the rapid evolution of phyla, and of class and ordinal types, as shown by Hyatt, the writer, and others. Indeed, it would seem as if the evclution and differentiation of varieties and species succeeded rather than preceded the formation of genera and higher groups. It may be questioned whether the natural selectionists could make any progress in evolution, so to speak, by beginning with merely simple variations, although after the higher or more general groups were originated, and this was by far the most difficult and important step, specific variations set in very rapidly, as early as Cambrian times. Few, except palæontologists, appear to appreciate the rapidity with which evolution in Precambrian and Cambrian times must have operated among the plastic forms which here and there crowded the early paleozoic seas.

Phylum III. MEROPODA. This group is proposed to include the classes of *Pauropoda*, *Diplopoda* and *Symphyla*.

Prosogoneate myriopods, in which the body is in the typical forms cylindrical, the trunk-segments variable in number, but usually numerous, and each segment "double" —*i. e.*, united by a dorsal plate, which was originally two plates which had been fused together (Heathcote), unless we adopt the views of Kenyon that the alternate plates disappeared, the remaining plates overgrowing those behind them, so as to give rise to the anomalous double segments; the feet arise close together along the median line of the body, there being no sternal plates between them. In the typical Diplopoda the head consists of three segments, the preoral or antennal and two postoral, bearing the mandibles (protomalæ) and the single pair of maxillæ (deutomalæ) united to form the gnathochilarium or underlip. As all the members of this phylum agree in having from two- to three-jointed mandibles, in which respect they differ from Chilopod Myriopods and especially insects, we have given the name *Meropoda* to this phylum in allusion to the primitive nature of these appendages, which resemble the maxillæ rather than the mandibles of insects.[1] The mandibles of the Diplopods consist of three segments, a basal segment (cardo), a middle segment (stipes), and a distal one (mala mandibularis), which supports two lobes homologous with the galea and lacinia of the maxilla of an insect. Diplopods are also provided with eversible coxal glands, in position like those of Scolopendrella; these perhaps functioning as blood-gills, and in Lysiopetalum occurring between the coxæ of the third to sixteenth pair of limbs.

A primitive feature, and the one diagnostic of the Meropoda as compared with the Chilopodous Myriopods, is the paired genital ducts and openings which are situated near the head between the second and third pair of legs. In the Symphyla the opening is single, proving the later origin of that group. Another diagnostic feature is that the male genital glands lie beneath, while in Peripatus, Chilopods and insects they lie above the digestive canal.

The tracheary system is also more primitive than in Chilopoda and insects, the tracheæ not being branched (except in Glomeridæ) and anastomosing, and the tracheæ themselves are without spiral threads (tænidia). In Diplopods the stigmata, which are permanently open, are placed beneath the legs, or even in the coxal joints. The nervous system is much more primitive than in Chilopoda and insects. The external genital armature, a complicated apparatus of male claspers and hooks, apparently arises from the sternum of the sixth trunk-segment, and they are modifications of the seventh pair of legs.

In their embryology the Diplopoda are more primitive than the

[1] There is an approach to this trimerous condition in Thysanura and Orthoptera (Blatta) and certain Coleoptera (see my *Text-Book of Entomology*, p. 60, also p. 12).

Chilopoda. In Polydesmus the method of formation of the blastoderm more resembles that of the Crustaceans and Arachnida than that of Chilopods.

The larva of the Diplopods, though bearing but three pairs of legs, differs from that of any insect in that these limbs are not appended to consecutive segments; either the second or the third segment in different species of Julus being legless, while in Blaniulus the legs are borne on segments 2 to 4 behind the head.[1] The new double segments with their two pairs of legs arise at successive molts, so that the animal undergoes a partial metamorphosis; while the Chilopods are hatched in the form of the adult, being polypodous.

Pauropoda. Nothing has been added to our knowledge of these forms since the publication of the thorough works on them by Kenyon and by Schmidt.

The group was regarded as an order (Pauropoda) by Lubbock. Kenyon, however, created the order *Protodiplopoda*, including in it Pauropus and Polyxenus.

The Pauropoda are regarded by Kenyon as degenerate Diplopods, owing to the absence of tracheal and circulatory systems, and distantly related to Polyxenus; on the other hand, the simplicity of the segmentation, the fact that there is but a single pair of legs to a segment, and other features pointed out by Kenyon, lead us to provisionally regard the group as a class more primitive and distinct from the Diplopoda. The number of mouth-appendages is the same as in the Diplopods; the genital aperture opens on the third trunk-segment, and the testis is situated above the intestine (the ovary below).

History of the Opinions regarding the Taxonomy of the Meropoda. —The first writer to doubt the naturalness of the group Myriopoda, and to state that the Chilopoda and Hexapoda were more nearly allied than the Chilopoda and Diplopoda, was Pocock,[2] in 1887. A year later Dr. Kingsley[3] arrived independently at the same opinion, adding the anatomical data in support of this view.

[1] The young of Polyzonium, however, is hatched with four pairs of legs, borne on each of the first four trunk-segments (Rimsky-Korsakow, *Travaux Soc. Imp. Naturalistes de St. Petersbourg*, xxv, 1895, Pl. 1, Fig. 8).

[2] *Annals and Mag. Nat. Hist.*, xx, October, 1887.

[3] *American Naturalist*, December, 1888, p. 1118.

In 1893 Pocock[1] divided the tracheate Arthropods into two sections, the *Progoneata* (including class Pauropoda and class Diplopoda), and *Opisthogoneata*, embracing the Homopoda (class Symphyla and class Chilopoda) and Hexopoda (class Hexopoda). Afterwards[2] he placed the Symphyla among the tracheate Progoneata.

This classification of Myriopoda was adopted by Schmidt in 1895, and has been adopted by Verhoeff[3] and the term Myriopoda will probably hereafter be merely used as a convenient appellation for polypod tracheate arthropods.

We would add that, rejecting the old term Tracheata, the prosogoneate Myriopods appear to us to constitute an independent phylum, rather than a subphylum, and for that reason we have ventured to propose the name *Meropoda* for the group (μερος, a part or segment; πους, ποδος, a leg), from the fact that the mandibles are more distinctly divided into segments than in any other group of Arthropods, thus more closely resembling the other appendages of the body, whence it follows that all the limbs, including the mandibles, have the primitive feature of being composed of several segments.

The Symphyla in respect to the structure of the mandibles are less primitive than the Diplopods, but I am now inclined to agree with those who have pointed out their Diplopods affinities and to place them among the Meropods.

The Systematic Position of the Symphyla.—This is a puzzling problem. In my *Text-Book of Entomology* I have with some care reviewed the chief points in the anatomy of Scolopendrella and the opinions of different authors regarding its systematic relations. Having studied sections of the animals, I prepared a figure or reproduction from the sagittal sections of a female, of which the accompanying illustration (Fig. 1) is an enlarged reproduction.

Comparing the digestive tract with that of Pauropus, it is divided into three portions; the œsophageal valve opening into the stomach is seen at *œ. v.*, and the beginning of the rectum is well marked; the two urinary tubes are large, arising at the posterior end of the intestine and ending in front at the third segment from the head

[1] *Zoologische Anzeiger*, xvi, Jahrg. 3, Juli, 1893, p. 271.

[2] *Natural Science*, x, February, 1897, p. 114.

[3] Bronn's *Klassen. u. ord. Thier-reichs*, Bd. V, VI, Abth. Arthropoda, Leipzig, 1902.

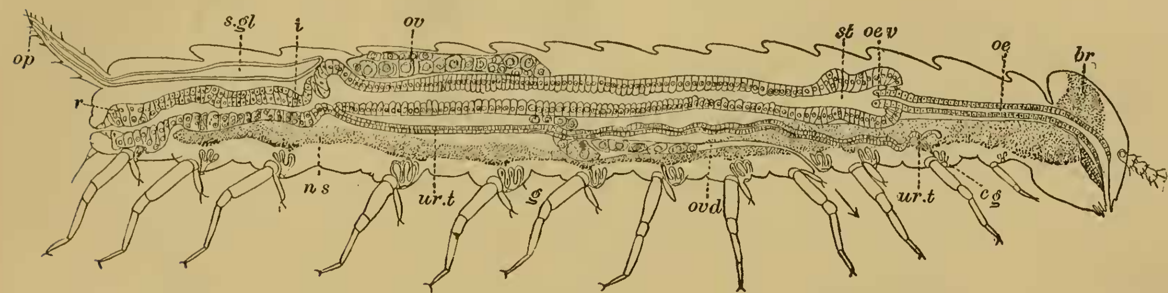

FIG. I. Section through *Scolopendrella immaculata*; *œ*, œsophagus; *œ.v*, œsophageal valve entering the stomach; *i*, intestine; *r*, rectum; *br*, brain; *ns*, abdominal chain of ganglia; *ovd*, oviduct; *ov*, ovary; *s.gl*, silk gland, and *op*, its outer opening in the cercus; *ur. t*, urinary tube; *cg*, coxal glands or blood-gills.—Author, *del.*

(*ur. t.*). The ovary (*ov.*) is seen to lie partly beneath but mainly above the intestine; the median opening of the oviduct (*ovd.*) being indicated by the arrow between the third and fourth pair of legs. Attention should be called to the eversible coxal sacs (*c. g.*), of which there are eleven pairs situated at the base of the legs of each pair; the sac is largest and most developed in the middle of the body and is a convoluted tube which makes three turns. The silk gland (*s. gl.*) at the end of the body is large, its direct opening situated at the end of the cercus, while the gland itself extends as far forward as the third segment from the end of the body. The brain and nerve-cord are large and thick, much as in Pauropus. The dorsal vessel, fat body, rectal glands and the salivary glands are not represented.

There is in Scolopendrella a mixture of Diplopod and Thysanuran characters, the former the more primitive and predominating. My original idea that it is a Thysanuran is certainly a mistaken one. The Symphyla evidently forms a group by itself, and I am inclined to agree with Pocock and with Kingsley that it should for the present be associated with Pauropods and Diplopods. Yet were it not for the anterior position of the genital opening we should regard it as the representative of a group from which the insects have descended.

The Symphyla is evidently a much less primitive group than the Pauropoda and Diplopoda, as proved by the single genital opening and the Thysanuran characters it possesses. It would seem as if it had already begun to diverge from the Diplopod stem, and was becoming modified in the direction of the Thysanura.[1] It is a true composite or prophetic type which has persisted from very early paleozoic times, and we may well imagine that there once existed a form intermediate between it and the Thysanura in which the genital outlet had moved back to the position it holds in Chilopods and insects. As I state in my *Text-Book of Entomology*, "certainly Scolopendrella is the only extant Arthropod which, with the

[1] The thysanurous characters and the fact that it has but a single pair of legs to a segment (unless, as Schmidt suggests, the parapodia "represent the vestiges of a second pair of legs and correspond to the hinder pair of limbs of the primary double segment," thus indicating I would add the diplopod origin of Scolopendrella) appear to indicate that it is a form which has become considerably detached from the Diplopod stem, and has gone part way towards the incoming Thysanura. Campodea also possesses these so-called "parapodia."